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Effects of Hypoxia and Low-Frequency Agitation on Byssogenesis in the Freshwater Mussel *Dreissena polymorpha* (Pallas)

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Abstract. The effect of variations in Po_2 and agitation rate on byssogenesis, motility, and survival of the zebra mussel (*Driessena polymorpha*) was investigated. Mussels exposed to a $Po_2 \leq 15.4$ torr exhibited increased mortality, reduced motility, and significant suppression of byssogenesis. At 7.7 and 15.4 torr, mean survival times were 5.2 and 5.8 days, maximum survival times being 15 and 16 days, respectively. After 21 days at a Po_2 of 23.1 torr, sample mortality was 33.3% and declined to 18.2% at 30.9 torr. There was no mortality at full air O_2 saturation (~154.3 torr). Adult zebra mussels exhibited the highest rate of byssogenesis in still water (0 cycles per minute [CPM]). Rate of byssogenesis progressively decreased as agitation rate increased. At 30 and 40 CPM, rate of byssal thread production was significantly lower than at 0 CPM. After 21 days, means of 58.6 and 44.8 byssal threads/mussel were found in the byssal mass of specimens exposed to 30 and 40 CPM, respectively, significantly fewer than the mean of 92.7 threads/mussel recorded in still water. Suppression of byssogenesis in *D. polymorpha* under hypoxic conditions is a response similar to that reported for the marine mytilid *Mytilis edulis;* however, suppression of byssogenesis with elevated agitation rate is the opposite response to that reported for *M. edulis.*

Introduction

The zebra mussel, *Dreissena polymorpha* (Pallas 1771), a freshwater bivalve mollusc, uses a byssus to secure to hard surfaces (Morton, 1969). The combination of a highly dispersive larval stage and retention of the byssal holdfast as an adult has made the zebra mussel a damaging macrofouling pest species in North America and Europe (Mackie *et al.,* 1989; Claudi and Mackie, 1993).

Several environmental factors influence the rate of byssogenesis in marine byssate mussels such as *Mytilus edulis* L., *Geukensia demissus* (Dillwyn), and *Perna indica* Kariakose and Nair. These include temperature (van Winkle, 1970), current velocity (Lee *et al.,* 1989), ambient oxygen concentration (Ravera, 1950; Reish and Ayers, 1968), agitation rate (van Winkle, 1970; Young, 1985), salinity (Young, 1985; Mathew and Fernandez, 1992), and seasonal variations in abiotic factors (Price, 1980, 1982). Changes in a mussel's ability to produce byssal threads can have far-reaching consequences; wave action and tidal rhythms continually subject intertidal inhabitants to strong mechanical forces, and high levels of mortality occur when mussels become detached from the substratum (Harger and Landenberger, 1971).

There is wide taxonomic separation between mytilid and dreissinid bivalves. They also have different evolutionary histories, one evolving in high-energy intertidal marine habitats, the other in low-energy freshwater habitats. Their contrasting evolutionary histories may have resulted in differences in how the physiological processes that regulate the rate of byssogenesis respond to changing environmental conditions (Clarke and McMahon, 1996a).

The effects of current velocity and temperature on the rate of zebra mussel byssogenesis have been previously quantified and compared to the responses of marine mytilids (Clarke and McMahon, 1996b, c). In this paper we investigate the effects of hypoxia and low-frequency agitation on byssal thread production by *D. polymorpha* and compare the results to data published for mytilid species.

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Materials and Methods

Specimen collection and maintenance

Specimens of *D. polymorpha* were collected from the upstream guide wall of Black Rock Lock, on the Niagara River, Buffalo, New York. They were transported overnight to The University of Texas at Arlington and maintained in aerated, dechlorinated tap water in a 280-l "Living Stream" holding tank at 5°C, without feeding, until used in experiments. Specimens have been maintained under these conditions with little mortality or loss of tissue mass for over 1 year (Chase and McMahon, 1994). Specimens of *D. bugensis* in the sample were visually identified according to descriptions by May and Marsden (1992) and removed. All specimens were used within 60 days of collection.

Responses to hypoxia

Prior to experimentation, mussels were acclimated in 17 l of aerated dechlorinated water to a test temperature of 25°C for 2 weeks. During acclimation, constant water temperature (±1°C) was maintained by holding aquaria in incubators. After acclimation, the byssus of experimental mussels was severed at the byssal gape with a razor blade. Immediately after byssus removal, mussels were placed on clear plastic plates (14 × 14 × 0.2 cm) located in the bottom of 17-l aquaria. Mussels were allowed to byssally reattach to the plastic plates for 12 h. The range of byssal thread production by individuals during the 12-h reattachment period was 4 to 26 threads/mussel.

Following the reattachment period, each plastic plate, together with either five or six attached mussels, was submersed in 4 l of dechlorinated tap water held in individual 5-l capped plastic chambers (22 × 22 × 12 cm) leaving 1 l of gas head-space. Water in these chambers was continuously bubbled with mixtures of oxygen and nitrogen gas. A Cameron GF-3 gas-mixing flowmeter regulated the gas mixture to maintain median dissolved oxygen partial pressures (Po_2) of 7.7 torr (5% air O_2 saturation at 25°C), 15.4 torr (10% air O_2 saturation), 23.1 torr (15% air O_2 saturation), 30.9 torr (20% air O_2 saturation) or 154.3 torr (100% air O_2 saturation). Media Po_2 was measured daily with a polarographic silver-platinum oxygen electrode (YSI Model 53). Chamber media were replaced every 2 days. The Po_2 of fresh medium was equilibrated to the experimental levels by perfusion with the appropriate gas mixture for 24 h before medium replacement.

Six chambers were used for each Po_2 treatment level, and the plastic plates were rotated among chambers daily. This rotation of specimens through the experimental chambers exposed individual mussels to each chamber in the rotation for an equivalent time period. Consequently, each mussel was exposed equally to any "tank effect" that may have been associated with a particular chamber in the rotation. This allowed each individual mussel to be treated as an independent, or "true," replicate in the statistical analysis.

Mean shell length (SL)—the greatest linear dimension from the tip of the umbos to the posterior margin of the shell—of the mussels used for each treatment was 17.8 mm (±3.2 SD, n = 28) at Po_2 = 7.7 torr; 15.4 mm (±2.7, n = 28) at 15.4 torr; 15.3 mm (±2.4, n = 28) at 23.1 torr; 17.4 mm (±2.9, n = 28) at 30.9 torr and 16.6 mm (±2.6, n = 48) at 154.3 torr.

The cumulative number of new byssal threads produced by reattaching mussels was recorded daily for 21 days after the initial reattachment (day 0). New byssal threads were counted by viewing the underside of the mussel, through the clear plastic plate, on a dissection microscope at 45×. Sites of thread attachment to the plate (*i.e.*, the plaques) were clearly visible when viewed in this manner. The location of new plaques was marked each day on the underside of the plate with a fine-tipped, waterproof, permanent ink marker. This procedure allowed quantitative determination of the effects of different Po_2 levels on byssal thread production. Time to mortality of individual mussels in the samples was recorded daily, as was time of any relocation of mussels on the plastic plates (detachment from the byssus followed by relocation and reattachment is common behavior among adults of this species, Mackie *et al.*, 1989).

The resulting data were tested for statistical significance by analysis of covariance (ANCOVA) in which Po_2 level was the main treatment, days was a repeated measure, and mussel SL and number of byssal threads present at day 0 were covariates. The null hypothesis that variations in oxygen partial pressure had no effect on the rate of byssal thread production was tested. A least significant difference (LSD) test was employed to detect any significant differences in rates of byssal thread production between experimental Po_2 levels.

Responses to low-frequency agitation

Specimens of *D. polymorpha* were acclimated and their byssus removed as previously described. Immediately after removal of the byssus, mussels were placed on clear plastic plates (7 × 7 × 0.2 cm) and allowed to byssally reattach for 12 h. The number of byssal threads produced by individuals during this period was 2 to 23 threads/mussel.

The plastic plate and attached mussel were then secured with a stainless steel spring clip to a fixed horizontal stage, supported from above and submerged in 15 l of dechlorinated tap water in a 17-l plastic aquarium. The

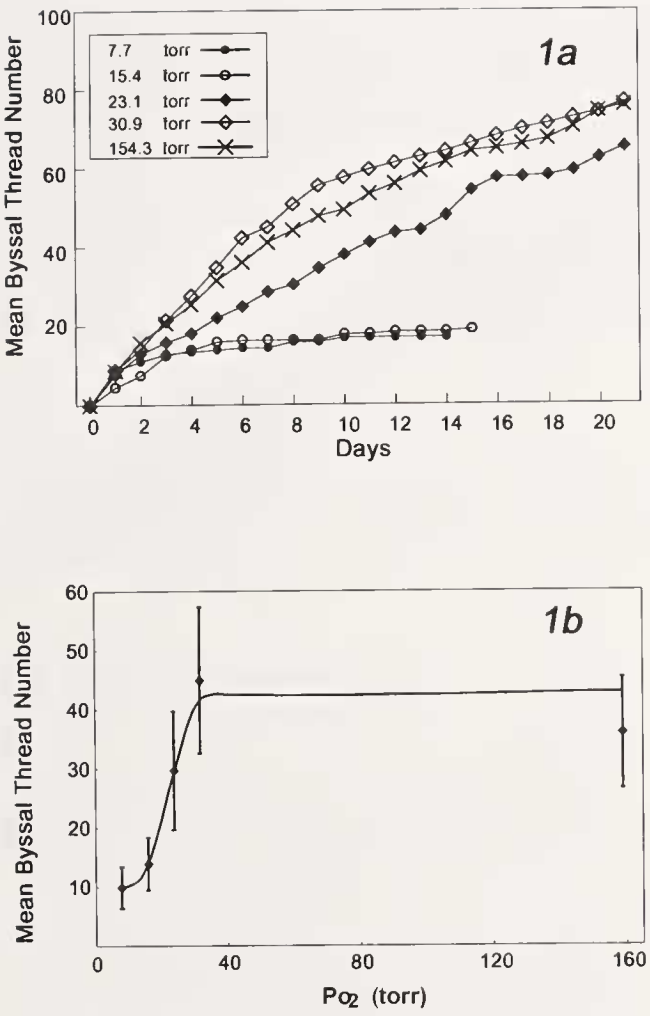

Figure 1. The effect of exposure to varying oxygen tensions on byssogenesis by specimens of the zebra mussel (*Dreissena polymorpha*) when exposed to Po_2 levels of 7.7, 15.4, 23.1, 30.9, and 154.3 torr. (a) Cumulative daily mean number of new byssal threads produced over a 21-day experimental period (or until 100% sample mortality). (b) Mean number of byssal threads (±95% confidence limits) produced in a newly formed zebra mussel byssal complex following 7 days of exposure.

aquarium was fixed on the reciprocating plate of a New Brunswick Scientific Co. water bath shaker (model RW-650). A constant water temperature (25°C) was maintained in the aquaria by using the temperature control system of the water bath. This arrangement made it possible to keep the submerged horizontal stage and attached mussel stationary while the water-filled aquarium was reciprocally displaced over a horizontal distance of 4 cm. The fluid medium in the aquaria was maintained at a depth of 10 inches and reciprocally displaced at a rate of 0 CPM (cycles per minute), 10 CPM, 15 CPM, 30 CPM, or 40 CPM. Frictional forces caused by water movement agitated the stationary mussel with a two-phase alternating force. Exposure of individual mussels was temporally separated to prevent pseudoreplication within treatments. The cumulative number of byssal threads produced by reattaching mussels exposed to varying agitation rates was recorded daily as previously described for specimens exposed to hypoxic conditions. Mussels were fed each day with rehydrated, washed, freeze-dried green algae, *Chlorella* sp., in recommended quantities (0.0032 g/mussel/day, Nichols, 1993). Medium was replaced every 2 days.

Before completion of the 21-day experimental period, some mussels spontaneously released from the byssus or were dislodged from their byssal hold-fasts by frictional forces caused by water movements. These individuals were not included in the calculation of mean daily byssal thread production. Rates of byssal thread production were calculated for mussels with mean SL of 21.9 mm (±4.1 SD, $n = 20$) at 0 CPM; 17.0 mm (±2.1, $n = 20$) at 10 CPM; 17.2 mm (±2.4, $n = 20$) at 15 CPM; 16.3 mm (±3.0, $n = 20$) at 30 CPM; and 16.4 mm (±3.1, $n = 10$) at 40 CPM.

Results were analyzed using a repeated measures ANCOVA. Agitation rate was the main treatment effect; mussel SL and number of byssal threads present at day 0 were covariates. The null hypothesis was that variations in agitation rate had no effect on the rate of byssal thread production by *D. polymorpha*. Because mussel SL was entered into the analysis as a covariate, and because a test for homogeneity of this covariate showed no significant differences between treatment groups, variation in SL between treatments was not considered to be a confounding element in the statistical analysis.

Results

Response to hypoxia

Over the 21-day experimental period, specimens of *Dreissena polymorpha* produced byssal threads at a slower rate when exposed to low Po_2 levels of 7.7 and 15.4 torr than at higher levels of 23.1, 30.9, and 154.3 torr (Fig. 1a). Repeated measures ANCOVA indicated

Table I

Repeated measures ANCOVA examining the effect of variations in partial pressure of oxygen (Po_2) and time (Days) on byssal thread production by Dreissena polymorpha *over a 7-day exposure period at 25°C*

Effect	df Effect	MS Effect	*F*	*P*
A) Po_2	4	7471	9.52	0.0001*
B) Days	6	5115	146	0.0001*
A × B Interaction	24	397	11.4	0.0001*

* Indicates a significant difference at *P* level shown.

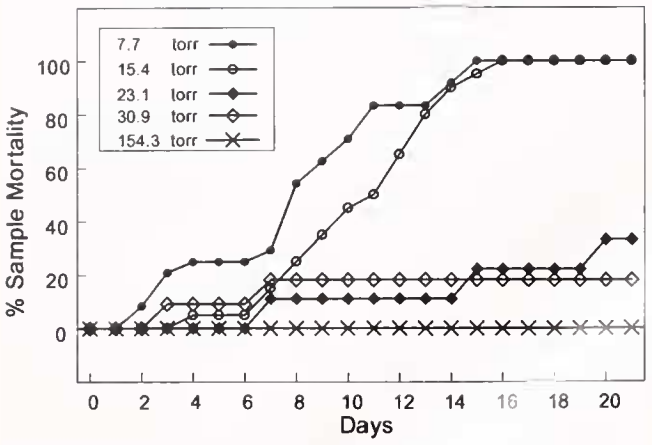

Figure 2. Daily mortality (as percentage of sample) of the zebra mussel (*Dreissena polymorpha*) when exposed to Po_2 levels of 7.7, 15.4, 23.1, 30.9, and 154.3 torr over a 21-day experimental period, or until 100% sample mortality occurred.

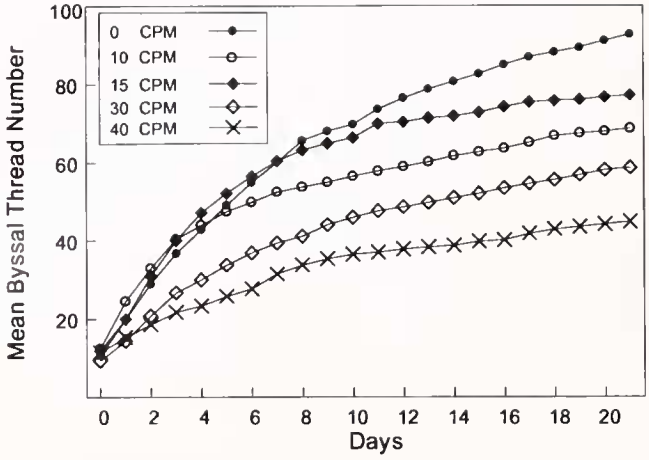

Figure 4. Cumulative daily mean number of byssal threads produced by specimens of the zebra mussel (*Dreissena polymorpha*) over a 21-day period, when exposed to agitation rates of 0, 10, 15, 30, and 40 cycles per minute (CPM).

that Po_2 significantly influenced the rate of byssogenesis over the first 7 days of exposure (Table I). An LSD test indicated that the mean rate of byssogenesis was significantly greater ($P < 0.05$) for mussels exposed to high Po_2 (23.1, 30.9, and 154.3 torr) than for those exposed to low Po_2 (7.7 and 15.4 torr), over the first 7 days of exposure (Fig. 1b). The null hypothesis that oxygen concentration had no effect on the rate of byssal thread production was therefore rejected. As a result of differing production rates, specimens held at 23.1, 30.9, and 154.3 torr had significantly more new byssal threads in their byssal mass after 7 days exposure than those held at 7.7 or 15.4 torr (Fig. 1b). Mean byssal thread number is reported after the first 7 days only, because high mortality in samples exposed to 7.7 and 15.4 torr led to increasingly large disparities in sample sizes between treatment groups as time progressed.

There was very little new byssal thread formation by zebra mussels exposed to 7.7 or 15.4 torr over the maximum survival times of 15 and 16 days. However, typical byssal thread production curves, showing a steady increase in the number of threads produced with time, were recorded at a Po_2 of 23.1, 30.9, and 154.3 torr (Fig. 1a). For mussels exposed to 7.7 or 15.4 torr, mean survival times were 5.2 and 5.8 days, and maximum survival times were 15 and 16 days, respectively. At 23.1 torr, 33.3% sample mortality was observed by the end of the 21-day experimental period. Mortality declined to 18.2% at a Po_2 of 30.9 torr. No mortality was observed in the sample of mussels exposed at 154.3 torr (Fig. 2).

At 7.7 torr, 14.3% of the sample released from the byssus, relocated, and byssally reattached within the experimental chamber prior to death or the end of the experimental period (whichever came first). This figure was 28.6% at a Po_2 of 15.4 torr, 67.8% at 23.1 torr, 53.6% at 30.9 torr, and 73.4% at 154.3 torr (Fig. 3).

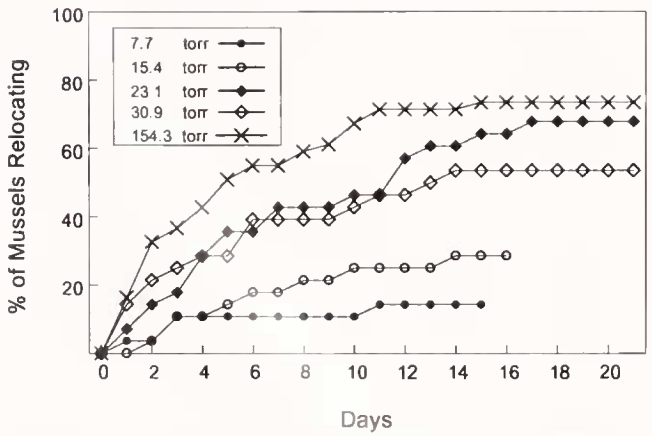

Figure 3. Percentage of the zebra mussel (*Dreissena polymorpha*) sample dropping from the byssal holdfast and relocating on the plastic plate, prior to death or the end of the 21-day experimental period (whichever came first), when exposed to Po_2 levels of 7.7, 15.4, 23.1, 30.9, and 154.3 torr.

Response to agitation

Byssal thread production was inhibited by increasing agitation rates. Maximal byssal thread production over the 21-day exposure period was achieved at an agitation rate of 0 CPM, and minimum thread production occurred at 40 CPM (Fig. 4). Repeated measures ANCOVA indicated that agitation rate had a significant effect on byssal thread production rate over the 21-day test period. This resulted in rejection of our null hypothesis. Production rate varied significantly with the re-

Table II

Repeated measures ANCOVA examining the effect of variations in agitation rate (CPM) and time (Days) on byssal thread production by specimens of Dreissena polymorpha *over a 21-day exposure at 25°C*

Effect	df Effect	MS Effect	*F*	*P*
A) Agitation	4	31595	3.19	0.0173*
B) Days	20	16354	162	0.0001*
A × B Interaction	80	423	4.20	0.0001*

* Indicates a significant difference at *P* level shown.

peated measures factor of days, indicating that the rate of byssogenesis changes over time. Significant interaction between these two variables suggested that the pattern of change in byssogenesis rate over time is influenced by agitation rate (Table II).

An LSD test indicated that byssal thread production rates at low levels of agitation (*i.e.*, 0, 10, and 15 CPM) did not differ significantly from each other, nor did production rates at the higher agitation levels (*i.e.*, 30 and 40 CPM). All significant differences occurred between these two subsets of observations. Over the 21-day exposure period, mean byssal thread production rate was significantly suppressed at 40 CPM compared with that at 0, 10, and 15 CPM (Table III).

ANCOVA examination of the number of byssal threads found in the newly formed byssal mass of specimens after 21 days of exposure to varying agitation rates indicated that there was a significant effect of agitation rate ($F = 4.86$, $P < 0.001$). Significantly fewer threads were formed by mussels exposed to 40 CPM than by those exposed to 0, 10, and 15 CPM. Conversely, significantly more byssal threads were formed after 21 days by mussels exposed to 0 CPM than by those exposed to 10, 30, and 40 CPM (Fig. 5).

Discussion

Responses to hypoxia

The physiological processes regulating the rate of byssogenesis by *Driessena polymorpha* appear to be hypoxia sensitive. Above 23.1 torr no suppression of byssogenesis was observed, but below 15.4 torr byssogenesis was significantly suppressed and sample mortality was 100%. A similar result has been reported by Reish and Ayers (1968) for the marine intertidal mytilid *M. edulis*. In this species, byssal thread production rates were normal at oxygen concentrations above 1 ppm (14.4 torr), but were inhibited by about 80% at $Po_2 \leq 1$ ppm, after 14 days of exposure.

A mean survival time of 82.8 h (range 34 to 156 h) has been reported for specimens of *D. polymorpha* acclimated to 25°C and exposed to acute hypoxic conditions (<3% of full air saturation, Matthews and McMahon, 1994). Survival times of only 24–48 h have been reported for mussels held at 23°–24°C under anoxic conditions (Mikheev, 1964). In our investigation, at low Po_2 levels mean survival time was 5 to 6 days, whereas at higher levels all or most of the sample survived the 21-day experimental period. Thus, although *D. polymorpha* appears to be capable of tolerating hypoxic conditions (≤15.4 torr) for longer periods than anoxia, there was very little difference in mean survival times at Po_2 levels ≤15.4 torr. The critical partial pressure of oxygen for both survival and byssogenesis of this species appears to lie somewhere between 15.4 and 23.1 torr.

The tendency for specimens of *D. polymorpha* to spontaneously release from the byssus and relocate to a new site declined with reduced oxygen concentration. While at elevated oxygen concentrations, mussels appeared to be very active. This suggests that motility and byssal thread secretion may be metabolically demanding activities for this predominantly sessile species. Such activities appear to be severely inhibited at oxygen concentrations below which efficient rates of aerobic metabolism cannot be maintained.

Responses to agitation

Increased levels of agitation resulted in a suppression of byssogenesis in the zebra mussel. This response is similar to that reported for the endobyssate estuarine mussel *Geukensia demissa* (Dillwyn) (van Winkle, 1970). This marine mytilid responded to agitation rates that gradually increased from 0 to 86 CPM by progressively decreasing byssal thread production (van Winkle, 1970). However, when the intertidal epibyssate bivalve *M. edulis* was agitated once every 4.5 s (about equivalent to an agitation rate of 10 CPM in our study), specimens responded immediately by increasing the rate of byssal thread production to a level of twice that recorded when agitated only once every 27 s (Young, 1985). Thus, both

Table III

Least significant difference (LSD) range test for significant differences in mean rate of byssal thread production between specimens of Dreissena polymorpha *exposed to agitation rates of 0, 10, 15, 30, and 40 cycles per minute (CPM) over a 21-day exposure period at 25°C*

Agitation Rate (CPM)	10	15	30	40
0	0.079	0.455	0.001*	0.001*
10		0.297	0.112	0.017*
15			0.008*	0.001*
30				0.260

* Indicates a significant difference at *P* level shown.

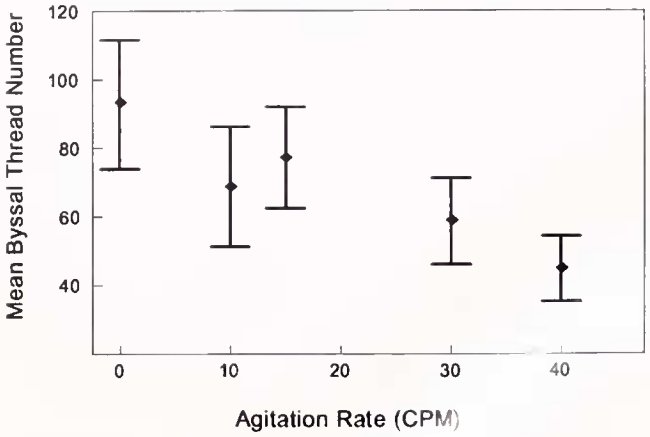

Figure 5. Mean number of byssal threads (±95% confidence limits) produced in a newly formed byssal complex of the zebra mussel (*Dreissena polymorpha*) following 21 days of exposure to agitation rates of 0, 10, 15, 30, and 40 cycles per minute (CPM).

D. polymorpha and *G. demissa* appear to respond differently than *M. edulis* to similar levels of elevated agitation.

These observations may possibly be explained by differences in the environments in which the three bivalve species have evolved. The zebra mussel is found in lotic and lentic systems in highest densities at depths greater than 3 m (Claudi and Mackie, 1993). Because the height of the vertical oscillation of waves is attenuated rapidly with depth (Wetzel, 1983), most zebra mussel populations probably reside below the depth of significant wave influence. Consequently, this species has not been exposed to the evolutionary pressures that would select for individuals that responded to wave agitation by increasing the rate of byssogenesis. This was demonstrated by our study, in which the highest level of byssal thread production was exhibited in still water. As levels of agitation progressively increased, mean rate of byssal thread production was suppressed. As a result, at 30 and 40 CPM the final number of threads found in the byssal mass was significantly reduced. This may explain why byssal thread production was inhibited in zebra mussels exposed to current velocities >0.2 m/s (Clarke and McMahon, 1996b)—the increased levels of agitation associated with high current velocity were responsible for the suppression.

Similarly, *Geukensia demissa* generally resides in estuarine mud flats, lying with most of its shell buried in the mud or gravel substratum and attaching byssal threads deeper in the sediment (Stanley, 1972). Consequently, like the zebra mussel, this species is not normally subjected to high levels of wave action or agitation.

In contrast to *D. polymorpha* and *G. demissa*, *M. edulis* inhabits a mechanically stressful, intertidal environment, and has evolved to increase the strength of the byssal attachment in response to increases in agitation. A strong attachment is essential to the survival of this intertidal species if it is to withstand the forces imposed upon it by heavy wave action (Young, 1985). Field observations support this hypothesis. Populations of *M. edulis* in wave-exposed habitats had a mean attachment strength 15 times greater than those from wave-protected habitats (Witman and Suchanek, 1984). Similarly, byssal attachment strength in this species increased in correlation with strong wave action associated with increased Atlantic winds (Price, 1982). Studies indicate that both the quantity and quality of the byssal threads produced by *M. edulis* change in response to elevated levels of wave action; specimens from a surf-exposed shore produced 56% more byssal threads, that were on average 28% stronger (individual thread tensile strength), than those produced by mussels from a sheltered bay area (Moore, 1979).

It is unclear why increased agitation inhibits byssogenesis in zebra mussels. A cresent-shaped region (or distal depression) at the terminal end of the ventral groove of the foot is responsible for plaque formation in *D. polymorpha* (Rzepecki and Waite, 1993). The end of the ventral groove on the foot of *M. edulis* must remain firmly pressed against the substratum for about 1 minute while the plastic rodlet of the byssal thread and the attached plaque cure and become coherent (Mercer, 1952; Price, 1983). Continuously high levels of mechanical disturbance may thus interfere with the zebra mussel's ability to maintain contact between the distal depression of the foot and the substratum long enough for a cohesive byssal thread to form. It has also been suggested that agitation of the soft siphon tissues by the frictional forces caused by moving water and air bubbles prevents the zebra mussel from opening its shell valves (Kaster, 1995). Because the foot cannot be extended when the valves are closed, the pedal activity necessary for byssal thread production would be inhibited. Byssal thread formation may also be inhibited by low food availability (Clarke and McMahon, unpub. data). Consequently, agitation-induced valve closure could indirectly inhibit byssogenesis by limiting the mussel's food consumption and assimilation rates.

Conclusions

Differences in the byssogenic responses of *D. polymorpha* and *M. edulis* may result from specific adaptations to their respective habitats. Because *M. edulis* inhabits high energy intertidal ecosystems, it has evolved to increase byssal thread production and strengthen the byssal attachment in response to elevated agitation. In contrast, *D. polymorpha* is a sublittoral species adapted

to life in relatively stable, large bodies of fresh water, usually at depths below 3 m (Claudi and Mackie, 1993). The tendency for agitation to suppress byssogenesis in *D. polymorpha* suggests that this species would be unlikely to form functional byssal holdfasts in wave-influenced littoral regions. In fact, we observed, but did not quantify, a clear tendency for increased numbers of zebra mussels to spontaneously release from the byssus when exposed to high levels of agitation. Thus, mussels initially settling in wave-influenced littoral regions may detach from original attachment sites and move to deeper waters. Dispersal of shallow-settling (<1 m) juveniles to greater depths has been reported for *D. polymorpha* (Mackie *et al.*, 1989). *M. edulis* occurs in both marine intertidal and estuarine habitats (Seed, 1976). In estuaries, it can periodically be subject to hypoxic conditions. As an adaptation, *M. edulis* is capable of good regulation of oxygen uptake with progressive hypoxia and has a high tolerance for hypoxia (Bayne *et al.*, 1976). In contrast, zebra mussels are relatively intolerant of anoxia or hypoxia compared to the majority of other marine and freshwater bivalve species (Matthews and McMahon, 1994) and display little or no capacity to regulate rate of oxygen uptake (Alexander and McMahon, unpub. data). The poor hypoxia tolerance of *D. polymorpha* prevents its penetration into oxygen-depleted hypolimnetic waters (Matthews and McMahon, 1994) and is reflected by inhibition of byssogenesis at oxygen concentrations higher than those reported to inhibit byssogenesis in *M. edulis* (Reish and Ayers, 1968).

These differences among the byssogenic responses of *D. polymorpha* and *M. edulis* to environmental variables suggest that such responses are likely to be species-specific and cannot be generalized across different taxonomic groups.

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